

BENTHIC PROCESSES IN SOUTH SAN FRANCISCO BAY: THE ROLE OF ORGANIC INPUTS AND BIOTURBATION

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Measurements of benthic processes over the last 13 years in South San Francisco Bay have spanned a range of hydrologic and water quality conditions. However, benthic fluxes of O_2 , NH_4^+ and NO_3^- have shown little variation. NH_4^+ and NO_3^- flux during this period were relatively constant in magnitude and direction. Sediment O_2 consumption was lower in the early 1980s than in the early 1990s. The reason for this difference is unclear, but may be a result of methodology or a lower density of the tube dwelling *Asychis elongata*. Although dissolved inorganic phosphate fluxes generally have been close to zero, in fall, there is a net flux into the sediments. Dissolved Si fluxes were consistently out of the sediments, while dissolved organic carbon fluxes were large and exhibited shifts in direction. Compared with other estuarine and coastal systems, temperature was not a major control on benthic fluxes because of the small annual temperature range. Irrigation by macrofauna enhances O_2 consumption and may control NH_4^+ fluxes in the shoals, where NH_4^+ flux was correlated with the biomass of mollusks. Porewater profiles of NH_4^+ , TCO_2 and radon suggest that irrigation is important in controlling dissolved constituent concentrations. Organic inputs such as deposition of phytoplankton may also affect benthic fluxes. In the channel, NH_4^+ flux was positively correlated to phaeopigment concentrations in sediments. Ratios of sediment O_2 consumption to DIN ($NH_4^+ + NO_3^-$) or DIP flux were very different than ratios of remineralization of organic matter with a Redfield ratio, and suggest that both denitrification and phosphorus burial were occurring at both locations.

Fluxes across the sediment-water interface represent an important linkage between benthic and pelagic environments. Nutrient fluxes out of sediments are often a significant nutrient source for water column phytoplankton production (Nixon 1981). Benthic fluxes may also respond to seasonal variations in productivity. This flux of materials is a result of a complex set of interdependent physical (diffusion, resuspension), chemical (sorption/desorption, complexation/dissociation, redox reactions, precipitation/dissolution), and biological (microbial transformations, bioturbation by benthic invertebrates and inputs of organic matter) components. Deposition of phytoplankton production and enhancement of benthic fluxes has been observed in many estuarine and marine ecosystems (Kemp & Boynton 1984; Jensen *et al.* 1990; Graf 1992; Grebmeier 1993). For example, O_2 consumption by sediments is affected by decomposition of organic matter and respiration by benthic invertebrates (Grebmeier 1993; Tahey *et al.* 1994). Similarly, NH_4^+ fluxes also reflect sediment processes such as NH_4^+ remineralization, nitrification and NH_4^+ excretion by macrofauna (Blackburn & Henriksen 1983; Henriksen *et al.* 1993), while NO_3^- fluxes are affected by nitrification, denitrification and NO_3^- concentrations. Phosphorus fluxes have been related to bottom water

oxygen concentrations (Kemp & Boynton 1992). Dissolved silica fluxes are controlled by bottom water silica concentrations and the chemical dissolution of biogenic silica (Conley *et al.* 1993).

San Francisco Bay is a highly urbanized estuary, surrounded by a population of approximately 5.8 million people. South San Francisco Bay (South Bay) is a lagoonal system in which the major input of freshwater and nutrients to the system comes from sewage treatment plants (Nichols *et al.* 1986; Hager & Schemel, this volume). South Bay is characterized by a broad expanse of shallow subtidal and intertidal areas. Approximately 80% of South Bay is ≤ 2 m deep (Fig. 1).

One of the most notable features of the South Bay ecosystem is the spring phytoplankton bloom. Phytoplankton growth is normally light-limited except in spring when tidal energy is reduced and persistent density stratification leads to phytoplankton blooms when chlorophyll *a* concentration exceeds $10 \mu\text{g l}^{-1}$ (Cloern 1991a). Phytoplankton, along with benthic algae, are the source of about 90% of organic carbon inputs to South Bay (Jassby *et al.* 1993). The benthic community seems to be major sink of phytoplankton production (Cloern 1982; Koseff *et al.* 1993). Although recent research in San Francisco Bay has emphasized this grazing link, less is known about the link between pelagic production and microbial processes in the sediments. This paper reviews benthic flux measurements made during three studies conducted in South San Francisco Bay between 1980 and 1993 and uses this record of benthic flux measurements to investigate the links between phytoplankton production and benthic processes.

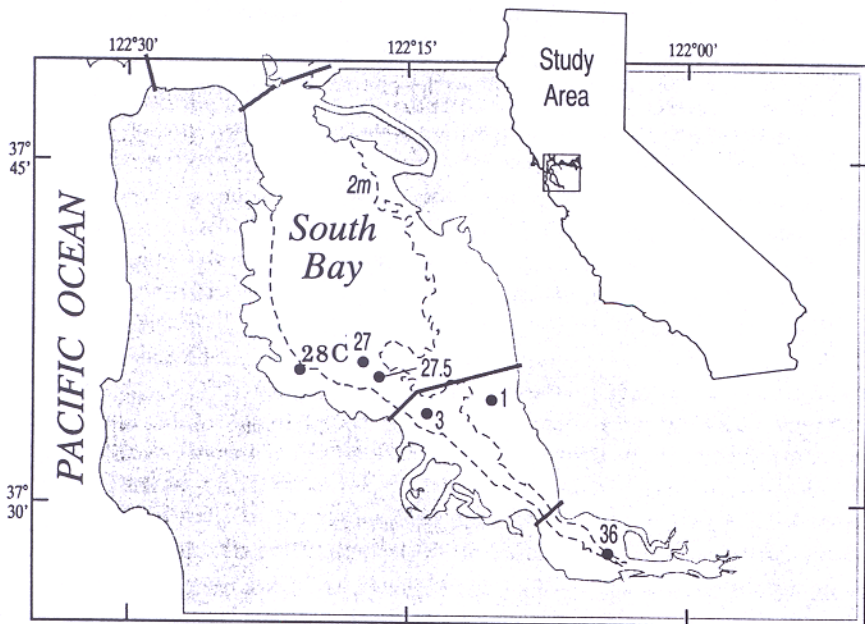


FIGURE 1. South San Francisco Bay location of stations and 2 m depth contour. Benthic flux measurements were made at stations 27.5 and 28C between 1980-1981, at stations 27, 28C and 36 in 1984, and at stations 1 and 3 between 1991-1993.

MATERIALS AND METHODS

Benthic fluxes in 1980-1981 were measured at two stations: 27.5 in the channel and 28C in the shoals of South Bay (Fig. 1). *In-situ* plexiglas chambers were used (Hartman & Hammond 1984) that trapped a 20 cm-high column of water overlying 1600 cm² of sediments. Samples were drawn three times during a deployment (0.2, 4 and about 20 hrs after emplacement). Measurements were also made in 1992 at stations 1 and 3 using a slightly different chamber design (Berelson *et al.* 1987). This device was PVC, trapped a 10 cm-high water column, covered 700 cm² of sediment, drew 6 samples during a 20 h deployment and measured oxygen with an electrode. In both chamber types, water was stirred continuously with a paddle. During a study in 1984, benthic fluxes were measured in cores at three stations (27, 28C, and 36) using a flow-through system as described in Miller-Way (1994). Benthic fluxes during 1991-1993 were measured as described below.

Benthic cores (12.1 cm diameter) were collected on the shoals (station 1) and in the channel (station 3) in South Bay (Fig. 1) with a modified dart corer. The corer and attached acrylic core tube were slowly lowered into the sediments to reduce the loss of the surface flocculent layer. Bottom water was collected at each station with a peristaltic pump from 0.5-1 m above the bottom. The cores were brought back to the lab in dark containers filled with water from the sampling site to minimize temperature changes. In the lab, overlying water was replaced with the bottom water, and cores were sealed with tops equipped with magnetic stirrers and gas-tight sampling ports. The height of water overlying the sediment ranged from 25-35 cm and sediment thickness ranged from 15-20 cm. Cores were incubated in the dark at ambient temperatures. Four water samples (30 ml) were removed at one hour intervals following an hour pre-incubation period. Water removed from the cores was replaced with bottom water. This resulted in a less than 1% dilution of the overlying water.

Water samples for O₂ analysis were stored unfiltered in glass bottles (7 ml) with Winkler reagents. O₂ concentrations were measured within 2 hrs of collection with an automated titration system (Metrohm 686™) using the potentiometric titration method of Graneli & Graneli (1991). Water samples for nutrient analysis were filtered (GF/F). NO₃⁻ and NH₄⁺ samples were initially frozen and analyzed on a Technicon II autoanalyzer within 2 months of collection. NO₃⁻ and NO₂⁻ (referred to as NO₃⁻) were analyzed by the automated Cd reduction method and NH₄⁺ by a modification of the salicylate-hypochlorite method (Hager 1993). Dissolved organic carbon concentrations were determined by ultraviolet/oxygen/persulfate oxidation (Hunter & Kuwabara 1994). Subsamples of wet sediment, approximately 8 g, from the top 1 cm were weighed, dried at 60°C for a minimum of 48 h and reweighed for calculation of percent water content. Porosity was determined using percent water content and assuming a sediment density of 2.7 g cm⁻³. Particulate C and N content were determined as described in Caffrey (1995). Following incubation, samples were taken from the cores for benthic chlorophyll *a* and phaeopigments. Cores were sieved through 0.55 mm screens to remove the infauna and the animals were preserved in 10% formalin for identification and weight

determination. Wet weights were converted to organic content using factors determined by Lie (1968).

RESULTS AND DISCUSSION

Benthic fluxes in South Bay have been measured periodically at shallow and deep stations between 1980 and 1993 (Table 1). Sediments at these stations tend to be fine grained with porosities ranging from 0.70-0.82 (Table 1). The particulate carbon (PC) content of the sediments at these stations ranged between 1.1 and 1.6%, while the range of particulate nitrogen (PN) content was between 0.12 and 0.27%. Station 1 is characterized by muddy sands with a lower PC and PN content, while stations 27, 28C, 27.5, and 3 have fine-grained sediments and higher PC and PN contents. Station 36 is closest to the major sewage treatment outfall in South Bay and has the highest PC and PN content.

TABLE 1. Years that benthic flux were measured in South San Francisco Bay, stations and methods, sediment characteristics: porosity, % carbon, % nitrogen

Year	Station	Water Depth (m)	Incubation Method	Average Porosity	% Carbon	% Nitrogen
1980-1981 ¹	27.5	14	<i>in-situ</i> chambers	0.75	1.38	0.16
	28C	2	"	0.70	1.41	0.15
1984	27	14	cores - flow through	0.81	1.43	0.18
	28C	2	"	0.77	1.41	0.16
	36	10	"	0.82	1.59	0.27
1991-1993	1	2	cores-batch ²	0.74	1.09	0.12
	3	13	"	0.80	1.44	0.14

¹ 1980-1981 data from Hammond *et al.* (1985).

² On one occasion in 1992, *in-situ* chambers were used in addition to core incubations.

During the 13-year period spanned by these studies, freshwater input from the Sacramento-San Joaquin Rivers to San Francisco Bay ranged from inputs less than 1000 m³s⁻¹ (between January and April) during the 1987-1992 drought and in 1981, to very high flow during 1982, 1983, 1986, and 1993 (Sheila Greene, pers. commun.). Benthic flux measurements have been made during low, intermediate and high flow years (as defined by Peterson *et al.* 1985, Table 2). River flow and increased stratification have been positively correlated with the spring phytoplankton biomass and productivity in South Bay (Cloern 1991b). Phytoplankton and benthic algae comprise about 90% of the organic carbon inputs to this area (Jassby *et al.* 1993). The highest levels of phytoplankton occur in spring when chlorophyll *a* levels increase from background levels of about 2 µg l⁻¹ to 25-50 µg l⁻¹ (Cloern 1987, 1991a and b, Table 2). Because the spring bloom is a well defined event which generally lasts between 2-4 weeks (Cloern 1991a), sedimentation of the spring bloom is most likely a relatively short, pulse input of fresh material to the sediments. The highest phaeopigment concentrations in the surface sediments as well as the greatest NH₄⁺ regeneration in sediments occur about a month after peak

TABLE 2. Year of benthic flux measurement, mean Sacramento and San Joaquin River Flow ($\text{m}^3 \text{s}^{-1}$) between January and April, and chlorophyll *a* concentrations ($\mu\text{g l}^{-1}$) averaged between March and April for the South Bay channel (USGS Hydrostations 24-36).

Year	River Flow $\text{m}^3 \text{s}^{-1}$	Mean Chlorophyll <i>a</i> concentration ¹ , $\mu\text{g l}^{-1}$
1980	2800	11.9
1981	500	5.4
1984	1300	7.6
1991	280	6.2
1992	380	8.0
1993	1570	16.5

¹ Chlorophyll *a* values are from Cloern (1991), Wienke *et al.* (1992, 1993), and Caffrey *et al.* (1994).

chlorophyll *a* concentrations in spring (Caffrey 1995). These results support the idea that sedimentation of the spring bloom is a fairly well defined event and that sediment properties may respond to it.

Sediment O₂ Consumption

O₂ consumption in sediments at the shoal stations were similar during the 1980-1981 and 1991-1992 sampling periods, while oxygen consumption was lower in the channel during the 1980-1981 period than during the 1991-1993 period (Fig. 2a). The average \pm s.e. oxygen consumption in 1980-81 at channel and shoal stations was 16 ± 7 and 30 ± 7 mmol O₂ m⁻²d⁻¹, respectively, and in 1991-93, it was 49 ± 3 and 47 ± 6 mmol O₂ m⁻²d⁻¹, respectively. The lack of sediment oxygen flux measurements for the period between 1981 and 1991 make it impossible to determine a reason for the higher oxygen consumption at the channel station in the 1990s. However, there are a number of factors which could contribute to these observed differences: different station locations, sediment type, organic inputs, types of incubations (*in-situ* chambers versus cores), and macrofaunal communities.

The channel stations 27.5 and 3 are approximately 8 km from one another. Water depths at these are similar, as are sediment porosity, PC, PN (Table 1) and percent mud (Nichols & Pamatmat 1988), suggesting that the physical characteristics of the sediments at these two station are similar. In addition, average spring chlorophyll *a* values for both time periods were similar, so it seems reasonable to assume that organic inputs from phytoplankton were comparable.

In April 1992, the comparison between *in-situ* chambers and core incubations at stations 1 and 3 demonstrated mixed results. Sediment O₂ consumption as measured with *in-situ* chambers was 28 ± 1 and 46 ± 7 mmol m⁻²d⁻¹ at channel and shoal stations respectively, while rates measured with core incubations were 43 ± 5 and 12 ± 2 mmol m⁻²d⁻¹ at the same channel and shoal stations respectively. No single factor can explain these differences. Fluxes measured with *in-situ* chambers may be higher than core fluxes because the cores can cut off or exclude deep

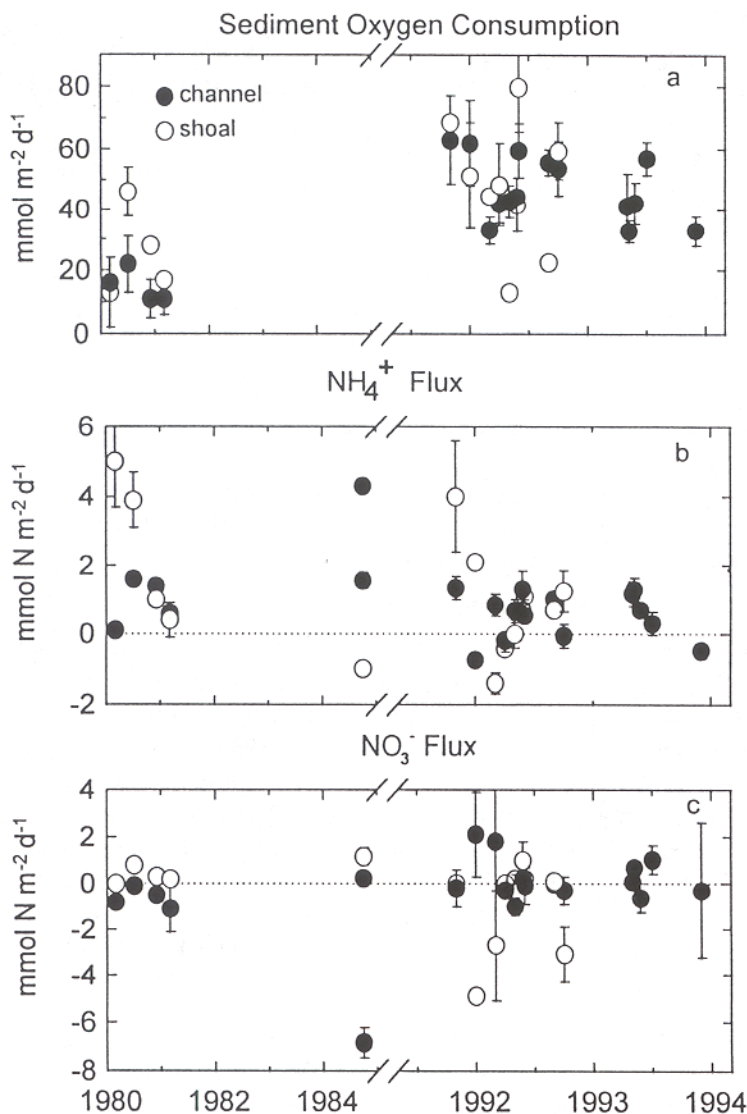


FIGURE 2. Sediment oxygen consumption in $\text{mmol O}_2 \text{m}^{-2} \text{d}^{-1}$ (a), NH_4^+ flux in $\text{mmol N m}^{-2} \text{d}^{-1}$ (b), and NO_3^- in $\text{mmol N m}^{-2} \text{d}^{-1}$ (c) at shoal (open circles) and channel (closed circles) stations in South San Francisco Bay between 1980 and 1993. 1980-1981 data is replotted from Hammond *et al.* (1985). + value is flux out of sediment for NH_4^+ or NO_3^- flux.

burrowing macrofauna. Irrigation by macrofauna such as *Asychis elongata* could be responsible for the higher fluxes from the chambers. If *in-situ* chambers should give higher rates of sediment O_2 consumption than core incubations because the *in-situ* chambers include macrofauna, this does not explain the difference between

1980s and 1990s values since the higher 1990s measurements were made with core incubations, not in-situ chambers.

Another difference between in-situ chambers and core incubations is the duration of the incubation. Samples are collected over a 20 hr period from the in-situ chambers, but usually over a 5-hr period from the cores. Sediment O₂ consumption is fairly linear over 5 hrs, but not for 20 hrs, so using a linear model to calculate SOC for a 20-hr period could underestimate the actual rate. For the longer incubation periods, a quadratic model may be more appropriate and was used to calculate rates for the *in-situ* chambers in April 1992. However, in 1980-81, SOC was calculated using a linear model, so this may explain the lower values during this period.

In addition, macrofauna densities were different between the 1980s and 1990s data, with greater densities of *Asychis elongata* at station 3 than station 27.5. Hammond *et al.* (1985) report that *Heteromastus filiformis* was the dominant tube dwelling polychaete at station 27.5. In San Francisco Bay, *Heteromastus* is considerably smaller than *Asychis* (Caffrey, unpublished data), so a community dominated by *Heteromastus* may not have the ability to enhance sediment O₂ consumption as much as *Asychis*.

There was no consistent seasonal pattern of O₂ consumption at either channel or shoal stations. Over the 13-year period, temperature was not significantly correlated with sediment O₂ consumption at either channel ($r = 0.39$, $p = 0.1$) or shoal stations ($r = 0.27$, $p = 0.28$). In contrast, O₂ consumption was correlated with sediment chlorophyll *a* concentrations ($r = 0.38$, $p = 0.009$, Table 3) and sediment phaeopigment concentrations ($r = 0.32$, $p = 0.03$) during 1991-1993. O₂ consumption was also related to the number, but not biomass, of annelids at the channel

TABLE 3. Correlation Coefficients between Benthic Fluxes: Sediment O₂ Consumption (SOC), NH₄⁺, NO₃⁻ and Selected Parameters: Temperature, Sediment Chlorophyll *a*, Sediment Phaeopigments, Macrofauna Biomass, Overlying water NH₄⁺ and NO₃⁻ Concentrations at Channel (3) and Shoal (1) Stations during 1991-1993. NS – not significant; first line – correlation coefficient; second line – *P* value.

	SOC	Channel NH ₄ ⁺ Flux	NO ₃ ⁻ Flux	SOC	Shoals NH ₄ ⁺ Flux	NO ₃ ⁻ Flux
SOC		0.27 0.02	NS		NS	NS
Temperature	NS	NS	NS	NS	0.81 0.001	0.45 0.005
Chlorophyll <i>a</i>	0.38 0.009	0.37 0.01	NS	NS	NS	NS
Phaeopigment	0.32 0.03	0.30 0.04	NS	NS	-0.51 0.02	NS
Macrofauna Biomass	NS	0.27 0.02	NS	NS	0.73 0.001	NS
NH ₄ ⁺ Concentration		NS			-0.66 0.001	
NO ₃ ⁻ Concentration			0.44 0.002			-0.49 0.003

station ($r = 0.36$, $p = 0.005$, data not shown). Annelids were the dominant invertebrate at this location, particularly *Asychis elongata* which can build tubes as long as 50 cm. Macrofauna enhance O_2 consumption through respiration and by increasing the sediment-water interface area through building tubes (Kristensen *et al.* 1991).

NH_4^+ Flux

NH_4^+ measurements usually indicated a flux out of the sediments (Fig. 2b) and were higher, on average, at the shoal stations (average 1.61 ± 0.47 mmol N $m^{-2}d^{-1}$) than at channel stations (average 0.57 ± 0.13 mmol N $m^{-2}d^{-1}$). In contrast to sediment O_2 consumption, NH_4^+ fluxes were similar over the 13-year period. NH_4^+ fluxes did not have consistent seasonal trends at either station (Fig. 2b). During 1991-1992 at the shoal station, the highest rates occurred in October, declined throughout the winter, became negative in February, and increased during spring, becoming positive in late April.

Although there was no apparent seasonal pattern at the channel station, NH_4^+ flux between 1991-1993 was correlated with concentration of benthic phaeopigments ($r = 0.30$, $p = 0.04$, Table 3) and benthic chlorophyll *a* concentrations ($r = 0.37$, $p = 0.01$, Table 3). Phaeopigment concentrations were particularly high in 1993 following the spring bloom (Table 4). Accumulation of phaeopigments in the channel may have been the result of trapping material from the shoals in the channel (Huzzy *et al.* 1990). Only a fraction of the organic matter that is remineralized in the sediments diffuses out as NH_4^+ flux. NH_4^+ remineralization in South Bay sediment was significantly correlated with water column chlorophyll *a* concentrations, suggesting a relationship between organic inputs (from phytoplankton production) and NH_4^+ remineralization (Caffrey 1995). However, on average, NH_4^+ flux out of the sediment was only 22% of NH_4^+ remineralization in the channel and 26% at the shoal station, suggesting that nitrification is a significant process in these sediments.

NO_3^- Flux

Mean NO_3^- fluxes varied from +2 to -6 mmol N $m^{-2}d^{-1}$ and were negligible for 18 of the 34 measurements (Fig. 2c). High NO_3^- fluxes into the sediment occurred at station 36 during the 1984 sampling period. This station is close to the discharge of the largest sewage treatment plant in South Bay. Nutrient concentrations in South Bay are usually highest at this station (Hager & Schemel, this volume) and were 115 μM during this sampling period. High NO_3^- fluxes into the sediment also occurred during December 1991 and February 1992 at shoal station 1 when bottom water NO_3^- concentrations were high, about 40 μM (Fig. 2c). NO_3^- fluxes were related to temperature and bottom water NO_3^- concentration at the shoal station (Table 3). This is consistent with the pattern of NO_3^- flux into the sediment during the winter when NO_3^- concentrations are high.

DIP and DSi Fluxes

Dissolved inorganic phosphate (DIP) fluxes were close to zero except during September 1984 (Fig. 3a). In September, DIP fluxes were negative with the highest

TABLE 4. Temperature, benthic chlorophyll *a*, phaeopigment, and macrofauna biomass from benthic flux stations in 1980-81 and 1991-93. Chlorophyll *a* and phaeopigment data for 1980-81 are from Thompson *et al.* (1981). n.d. — no data

Station	Season	Temperature °C	Chlorophyll <i>a</i> µg cm ⁻²	Phaeopigment mg cm ⁻²	Macrofauna Biomass gC m ⁻²
27.5	Winter '80	12	n.d.	n.d.	n.d.
	Summer '80	17	0.0	25.4	n.d.
	Fall '80	17	0.0	9.5	n.d.
	Winter '81	12	0.0	13.0	n.d.
28	Winter '80	12	n.d.	n.d.	n.d.
	Summer '80	17	4.7	37.9	n.d.
	Fall '80	16	7.4	42.5	n.d.
	Winter '81	12	1.1	19.4	n.d.
3	Fall '91	20	n.d.	n.d.	7.8
	Winter '91	13	2.5	33.4	6.3
	Spring '92	18	4.5	40.6	4.1
	Summer '92	21	7.2	36.4	14.3
	Fall '92	20	1.3	27.8	15
	Spring '93	16	4.4	131.2	12.6
	Fall '93	18	3.2	33.4	7.7
	Fall '91	20	n.d.	n.d.	31.9
1	Winter '91	13	3.7	63.5	7.3
	Spring '92	18	11.1	49.7	2.6
	Summer '92	21	7	51.4	10.3
	Fall '92	20	18.6	70.6	14.7

rates at station 36. This is consistent with the negative NO_3^- fluxes at this station and probably the result of high nutrient concentrations in the water column. DIP concentrations at station 36 were 35 µM, while concentrations at the other benthic flux stations in September 1984 were between 4-7 µM. The consistently low or negative DIP fluxes contrasts with the patterns observed in other estuaries, where high DIP fluxes out of sediment occur when sediment redox conditions drop (Kemp & Boynton 1984; Hopkinson 1987; Koop *et al.* 1990; van Duyl *et al.* 1993).

Dissolved silica (DSi) fluxes were positive with values ranging between 2 and 12 mmol Si m⁻²d⁻¹, except in February 1980 when fluxes were into the sediments (Fig. 3b). No seasonal pattern was apparent in the channel. In the shoals, DSi fluxes were highest in June. This may be because biogenic silica regeneration in sediments is a predominantly chemical process which is determined by a combination of factors including porewater silica concentrations, temperature, pH, and salinity (Conley *et al.* 1993). DSi fluxes also reflect irrigation by macrofauna (Hammond *et al.* 1985).

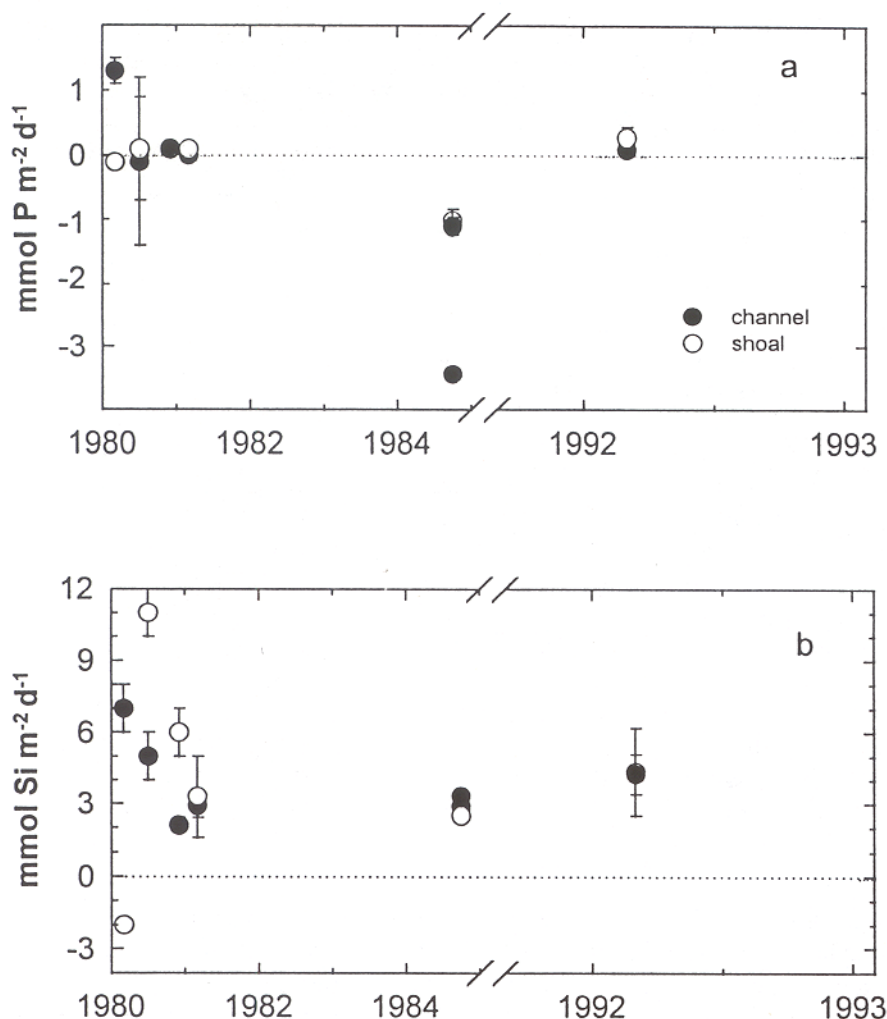


FIGURE 3. Seasonal variation in DIP flux in $\text{mmol P m}^{-2} \text{d}^{-1}$ (a), DSi flux in $\text{mmol Si m}^{-2} \text{d}^{-1}$ (b) at shoal (open circles) and channel stations (closed circles) in South San Francisco Bay. 1980-1981 data is replotted from Hammond *et al.* (1985). + value is flux out of sediment.

DOC Flux

The seasonal pattern in dissolved organic carbon (DOC) fluxes was quite variable between 1992 and 1993. During spring of 1992, DOC fluxes were negative in February and changed to positive fluxes by April with highest positive DOC flux at the channel station in the fall (Fig. 4). The seasonal pattern of DOC fluxes at the shoal station was similar to the channel station except that fluxes were near zero in September. The pattern of DOC fluxes in the channel was quite different during 1993. During this year, fluxes decreased during the spring and were negative in the

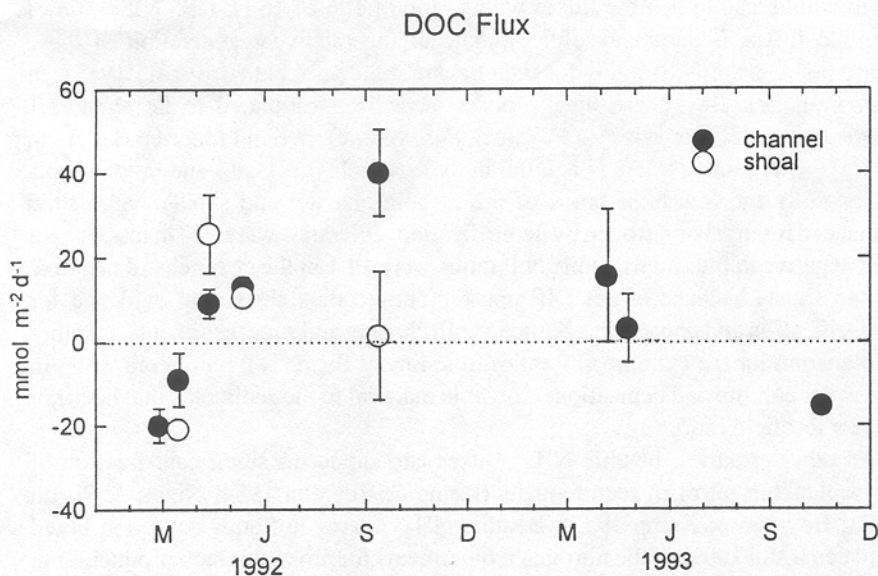


FIGURE 4. Sediment DOC fluxes in $\text{mmol m}^{-2} \text{d}^{-1}$ at shoal and channel stations in South San Francisco Bay between 1992 and 1993. + value is flux out of sediment

fall. Despite the higher water column chlorophyll *a* concentrations in 1993 than 1992, DOC fluxes at the channel station in April were similar. Average DOC fluxes in the shoals and channel are about 5% and 10% of the average sediment O_2 consumption at these stations, respectively.

Uptake of DOC by sediments has not been reported for other marine sediments (Burdige *et al.* 1992, and references therein). DOC fluxes in other coastal environments range from 0.55 to 6.0 $\text{mmol m}^{-2} \text{d}^{-1}$ (Burdige *et al.* 1992) and have usually been determined based on porewater gradient calculations. In contrast, the 1992 and 1993 flux core experiments: (1) include bioturbation effects, (2) do not impose diffusion coefficients for flux determinations, but (3) assume that physical stirring of the core overlying water reasonably represents natural hydrodynamic conditions. Uptake of DOC by heterotrophic bacteria has been observed in the open ocean and lakes (Kirchman *et al.* 1991; Sundh 1992). Although DOC uptake by heterotrophic bacteria has not been reported in sediments, this process may be responsible for the observed uptake measurements from San Francisco Bay. In addition, macrofauna, including cnidarians, polychaetes and bivalves, may utilize DOC (Wotton 1991; Neira & Hopner 1994), so uptake by benthic macrofauna represents another potential mechanism to explain our measurements.

Benthic-Pelagic Coupling

Deviations of flux ratios, such as O:N or N:P, from Redfield ratios have often been attributed to processes such as denitrification, or enhanced burial of phosphorus (Nixon 1981; Boynton & Kemp 1985; Hammond *et al.* 1985; Hopkinson 1987; Teague *et al.* 1988). Benthic remineralization of organic matter with a Redfield

ratio would lead to benthic fluxes with a ratio of 106 C: 16 N: 1 P. N:Si ratio of benthic fluxes is another useful estimate of the relative regeneration of these nutrients. Uptake N:Si ratios for diatoms are quite variable (Brezinski 1985). In San Francisco Bay, these uptake ratios have been estimated to be about 1:1 (Peterson *et al.* 1985; Hager & Schemel, this volume). In San Francisco Bay, high average O:N ratios (where N is DIN) in the channel (O:N = 66) and in the shoals (O:N = 58) and low N:Si ratios of 0.2 in both channel and shoals suggest the enhanced removal of nitrogen by denitrification. O:P ratios were 932 in the channel and negative in the shoals, while N:P ratios were 14.1 in the channel and negative in the shoals because of net DIP uptake. These ratios are strong evidence for denitrification and phosphorus burial in both channel and shoal sediments. Another explanation for the extreme O:P ratios in sediment fluxes is P remineralization in the water column and deposition of organic material to the sediments that does not have a Redfield ratio.

In other estuaries, benthic NH_4^+ fluxes can support a significant fraction of phytoplankton nitrogen requirements (Kemp & Boynton 1984; Nixon & Pilson 1983; Boynton & Kemp 1985). Benthic NH_4^+ fluxes in South Bay contributed between 0 and 100% of the nitrogen requirements for phytoplankton production in the channel depending on the season (Table 5). In the spring (March-May) when phytoplankton N demands are greatest, NH_4^+ fluxes were able to satisfy between 6 and 12% of phytoplankton N demand. In contrast, NH_4^+ fluxes during the fall period could often meet > 80% of potential phytoplankton nitrogen demand. This contrasts with the pattern observed in the Patuxent River where regeneration could supply over 60% of phytoplankton nitrogen requirements, except in the winter (Kemp & Boynton 1984). Similar estimates can be made for P and Si demand by phytoplankton. DSi fluxes can supply about 22% of the Si requirement of phytoplankton in the spring (assuming a C:Si ratio of 5.3), and about 100% of phytoplankton requirements in most other months. DIP fluxes were quite variable, and able to supply between 0 and > 100% of potential phytoplankton P requirements.

Influence of Macrofauna

A major change in the macrofauna community occurred between the early 1980s and 1990s with the introduction of *Potamocorbula amurensis* (Carlton *et al.* 1990). *Potamocorbula* was able to displace much of the resident bivalve community (Nichols *et al.* 1990), although it seems to have had less of an effect in channel sediments dominated by *Asychis elongata* (J. Thompson, pers. commun.). Stations 27.5 and 28C, occupied during the early 1980s, had very high densities of *Heteromastus filiformis* and *Asychis elongata*, respectively. Burrow densities of 1,000 to 7,000 m^{-2} were reported at these stations (Hammond *et al.* 1985).

At shoal station 1, NH_4^+ flux was correlated with the biomass of mollusks ($r = 0.79, p < 0.001$, Fig 5). This suggests that NH_4^+ excretion or irrigation of sediments by mollusks is a significant component of NH_4^+ flux out of sediments. In the channel during the 1991-1993 sampling period, NH_4^+ fluxes and macrofauna biomass were also correlated ($r = 0.27, p = 0.02$). Similar relations between macrofauna biomass and NH_4^+ flux have been observed in other systems (Blackburn &

TABLE 5. Estimated contribution of benthic flux to nutrient demands of phytoplankton in South San Francisco Bay

Date	Phytoplankton Production ¹ (mg C m-2d-1)	Phytoplankton Requirements ² (mmol m ⁻² d ⁻¹)			Benthic Flux (mmol m ⁻² d ⁻¹)			Nutrient Supplied %		
		N	P	Si	NH ₄ ⁺	DIP	DSi	N	P	Si
Winter (Dec-Feb)										
Feb 80	124	1.57	0.1	2.0	0.1	1.3	7.9	6	> 100	> 100
Feb 81	99	1.25	0.1	1.6	0.6	0.0	2.9	48	0	> 100
Dec 91	78	0.98			-0.74	n.d.	n.d.	< 0		
Feb 92	120	1.51			0.84	n.d.	n.d.	56		
Spring (Mar-May)										
Mar 92	332	4.19			-0.18	n.d.	n.d.	< 0		
Apr 92	1213	13.32	1.0	19.1	0.99	0.1	4.2	6	10	22
May 92	439	5.54			0.53	n.d.	n.d.	10		
Apr 93	678	8.56			1.05	n.d.	n.d.	12		
May 93	303	3.83			0.3	n.d.	n.d.	8		
Summer (Jun-Aug)										
Jun 80	341	4.31	0.3	5.4	1.6	-0.1	5.0	37	< 0	93
Jul 92	497	6.27			1.01	n.d.	n.d.	16		
Fall (Sep-Nov)										
Nov 80	113	1.42	0.1	1.8	1.4	0.1	2.1	98	100	> 100
Sep 84	334	4.22	0.3	5.2	-0.98	-1.1	3.3	< 0	< 0	64
Oct 91	187	2.36			1.84	n.d.	n.d.	78		
Sep 92	205	2.59			-0.06	n.d.	n.d.	< 0		

¹ Net phytoplankton production in photic zone calculated using equation 5 from Cloern (1991a) with average monthly chlorophyll *a* concentrations, a mean attenuation coefficient of 1.8 and average monthly irradiance from Redwood Creek (B. Cole, pers. commun.).

² Phytoplankton nutrient requirements were estimated using Redfield ratios (C:N = 6.6, C:P = 106, C:Si = 5.3).

³ n.d. = no data.

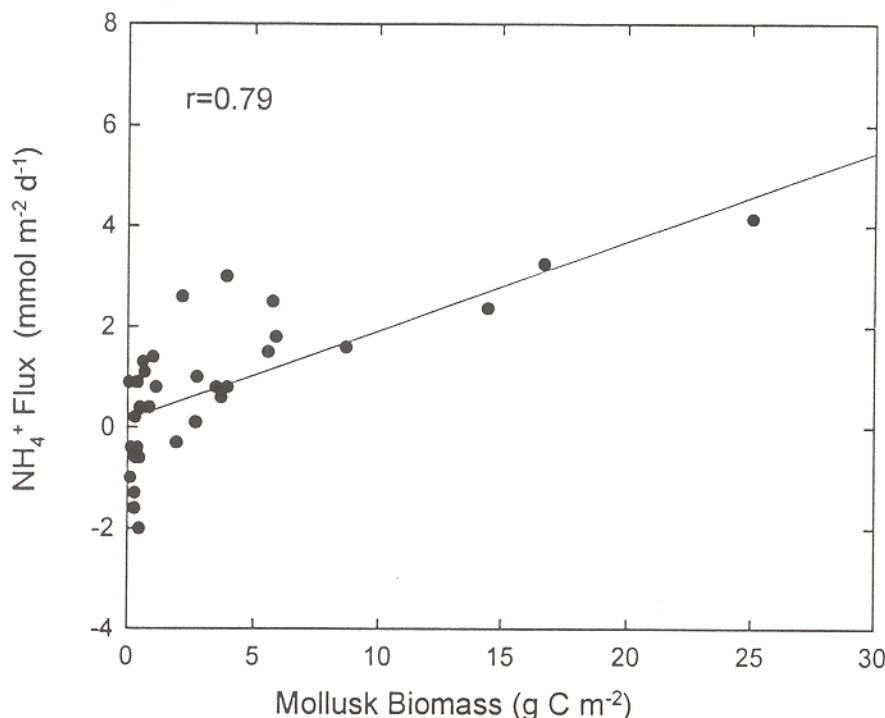


FIGURE 5 Ammonium flux versus mollusk biomass at shoal station (1) between 1991-1992.

Henriksen 1983; Matisoff *et al.* 1984; Lomstein *et al.* 1989; Kristensen *et al.* 1991; Henriksen *et al.* 1993). Excretion of NH_4^+ by mollusks can also have a significant impact on benthic fluxes and porewater profiles (Yamada & Kayama 1987). Porewater profiles of NH_4^+ and radon throughout South Bay change little with increasing depth in sediment, particularly in areas with higher macrofauna densities (Hammond *et al.* 1985; Caffrey 1995). Mollusks dominate benthic biomass in South Bay, although densities of tube dwelling polychaetes like *Asychis elongata* can be high (Nichols & Pamatmat 1988; Hammond *et al.* 1985). During the 1991-1993 study period, mollusks dominated at station 1 in the shoals, while polychaetes dominated station 3 in the channel (Caffrey, unpublished data). Irrigation of tubes and burrows can have a great influence on porewater concentrations (Aller 1982; Hammond *et al.* 1985; Aller 1988).

SUMMARY

In South Bay, the response of benthic fluxes to the spring phytoplankton bloom and phytoplankton deposition seems muted, compared to other estuarine and marine systems (Jensen *et al.* 1990; Grebmeier 1993). South Bay also seems to function quite differently than Tomales Bay where benthic fluxes had a strong seasonal pattern, with highest rates in later summer during peak temperatures

(Dollar *et al.* 1991). Tomales Bay differs from South Bay by having a summer peak in primary productivity, runoff from an agricultural watershed, smaller percentage of shallow water, and no large riverine inputs. These differences may contribute to the differences in benthic flux pattern.

It is difficult to determine whether benthic fluxes have changed significantly over this 13 year period because of the few numbers of measurements. NH_4^+ , NO_3^- , DIP and DSI fluxes are all quite similar despite changes in station location and method of sampling. In contrast, SOC is much higher in recent years than in the 80s. Carbon inputs from phytoplankton have not changed during this time period (Table 2). Differences in methodology, specifically the length of incubation, may be responsible for these differences, as well as a difference in biomass of tube-dwelling macrofauna such as *Asychis elongata*.

In 1992, there was no enhancement of sediment oxygen consumption following peak chlorophyll *a* levels, although sediment oxygen consumption did increase following the spring bloom of 1993 (Fig. 2a). DOC fluxes during the 1992 and 1993 spring blooms were similar despite much higher productivity in 1993. In addition, the significant correlations between sediment oxygen consumption, NH_4^+ flux and benthic chlorophyll *a* at channel station 3 suggests a link between phytoplankton production and benthic processes (Table 3). However, it seems clear that better spatial and temporal coverage of benthic fluxes is necessary in order to understand the coupling between benthic and pelagic systems in South Bay.

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SAN FRANCISCO BAY: THE ECOSYSTEM

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